ORIENTATION AND VARIABILITY IN THE OSSICONES OF AFRICAN SIVATHERIINAE (MAMMALIA : GIRAFFIDAE)

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(With 5 figures)

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INTRODUCTION

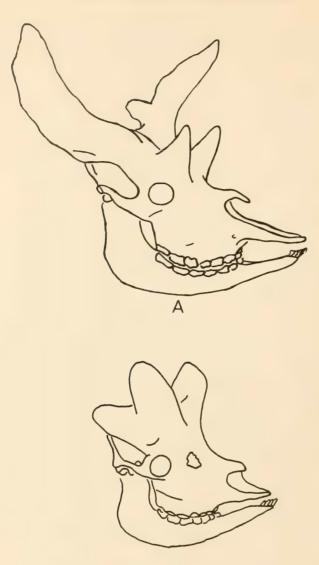
Singer & Boné (1960) placed most of the Plio-Pleistocene sivatheriines from Africa in the species *Sivatherium olduvaiense*. In addition they recognized *Libytherium maurusium*, founded on a right mandible from Garet Ichkeul, St. Arnaud (Tunisia) and a second species of *Sivatherium*—*S. cingulatum*—based on dental material from South Africa. There seems to be some controversy over the correct identification of the common African sivathere, *Sivatherium olduvaiense* being used by Hopwood (1934) and Singer & Boné (1960) while *Libytherium olduvaiensis* was preferred by Leakey (1965). Arambourg (1960) concluded that *Libytherium maurusium* was conspecific with *Sivatherium olduvaiense*. If Arambourg's interpretation is correct, the genus *Sivatherium* (Falconer & Cautley, 1836) has priority over *Libytherium* (Pomel, 1892) but the species *Sivatherium olduvaiense* is a junior synonym of *Sivatherium maurusium* (Pomel, 1892).

There would, therefore, appear to be two species of Sivatherium from Africa-S. maurusium and S. cingulatum. A third (and the type) species of Sivatherium-S. giganteum-is known from the Siwalik Series of India.

Sivatherium giganteum has four ossicones (or horns) in the male, an anterior conical pair arising from the frontals and a posterior palmate pair situated on the parietals. The females are believed to lack ossicones. S. giganteum thus differs from other genera of Asian sivatheres with ossicones. Bramatherium also has four ossicones—two extending upwards from the fronto-parietal region and two extending laterally from the parietals but, in contrast to Sivatherium, the anterior ossicones are much larger than the posterior pair. Hydaspitherium has one pair of ossicones only, fused at their base into one solid mass, on the fronto-parietal region. Birgerbohlinia, the only European sivathere, possesses a single

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Fig. 1 A. Skull of *Sivatherium giganteum* (after Colbert 1935). B. Skull of *Bramatherium* (after Colbert 1935).

pair of ossicones that are aligned vertically and are rounded in cross-section. Because of the incomplete nature of the African sivatheriine material it has been tempting to orientate the ossicones of the African specimens similarly to those of the Asian *Sivatherium giganteum*. The discovery at East Rudolf, Kenya,

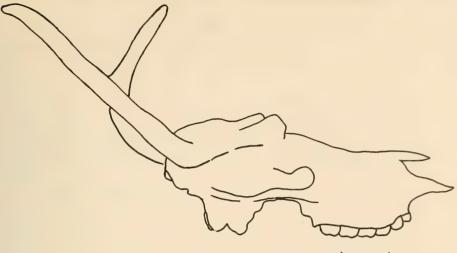


Fig. 2 Sivatherium skull from East Rudolf, Kenya. Scale = 10 cm.

of a virtually complete cranium of *Sivatherium* (Harris in press) has proved of great importance for reinterpreting incomplete ossicones found at other Plio-Pleistocene sites in Africa (Arambourg 1948, 1949; Singer & Boné 1960). The posterior ossicones of the East Rudolf skull are orientated in an entirely different direction from those of *S. giganteum*. Re-examination of ossicones from Olduvai Gorge, Tanzania, has shown that some of the more complete specimens were orientated in accordance with the East Rudolf skull and it is likely that other specimens must be similarly aligned. Some doubt is also thrown on whether the anterior ossicones of the African sivatheriines are in fact separate entities from the posterior ossicones.

POSTERIOR OSSICONES

Two of the Olduvai *Sivatherium* ossicones (Old.1.53 of Singer & Boné (1960) and FLKS 1) extend proximally to include parts of the nuchal crest and may therefore be confidently orientated in light of the East Rudolf skull. Together, these three specimens provide a basis for orientation of other, less complete ossicones. Four factors appear to be of use in orientation—tuberosities, grooves, torsion and cross-section shape.

Tuberosities

Although the posterior ossicones of the African sivatheriines appear to be markedly less palmate than *S. giganteum*, they are ornamented by a flange or flanges and a number of discrete knobs. This ornamentation occurs on the anterior (or distally and, where affected by extreme torsion, lateral) surface of

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the ossicone. Discrete knobs have been observed diametrically opposite to the proximal flange in the proximal part of the ossicone but are smaller and fewer in number than on the anterior surface; distally the knobs appear to be confined to one edge.

Grooves

Longitudinal or oblique grooves are often present on the ventral surface of the ossicones. Such grooves differ markedly in development; on some specimens they are very faint, in others they are present on the dorsal surface also. Where grooves are present on both surfaces the dorsal grooves are always distinctly fainter and less numerous than those on the ventral surface.

Cross-section

The ventral surface of the ossicone is normally distinctly more convex than the dorsal surface, especially in the proximal portion.

Torsion

Some sivatheriine ossicones are almost straight, but, where present, torsion is always clockwise from the base outwards on the right ossicone and anticlockwise on the left (cf. Singer & Boné 1960: 494).

Even on incomplete ossicones a combination of the above features normally serves to orientate the specimen correctly. In view of the above, the following corrections are necessary to plates illustrating Singer & Boné's (1960) monograph:

Plate	Specimen	Side	Stated View	Corrected View
1 <i>a</i>	Old.2.53	right	anteromedial	ventral
1 <i>b</i>	Old.86	left	anteromedial	lateral
1 <i>c</i>	Old.1.53	left	anteromedial	anteroventral
1d	Old.2.53	right	posterolateral	dorsoposterior
1 <i>e</i>	Old.1.53	left	posterolateral	posterior
1f	Old.86	left	posterolateral	dorsal
2a	Old.3.53	right	posterolateral	dorsal
2b	Old.3.53	right	anteromedial	ventral
2c	Old.3.53	right	anterior	lateral
3 <i>a</i>	M.14955	right	posterodorsal	dorsal
3 <i>b</i>	M.14955	right	anteromedial	ventral
3 <i>c</i>	Old.52 SHK/BKII+M.14594b	right	anteromedial	ventral
3 <i>d</i>	Old.52 SHK/BKII+M.14594b	right	posterolateral	dorsal
29 <i>c</i>	C.431A	right	anterior	anterior
29 <i>d</i>	C.431A	right	anteromedial	ventral
43a	Hopefield 4372	right	posterolateral	dorsal
43 <i>b</i>	Hopefield 4372	right	anterior	anterior
43 <i>c</i>	Hopefield 4372	right	anteromedial	ventral
44a	Hopefield 4373	left	anteromedial	ventral
44 <i>b</i>	Hopefield 4373	left	anterior	anterior
44 <i>c</i>	Hopefield 4373	left	posterolateral	dorsal
51a	St Arnaud, Algeria 1948–1–2	right	anteromedial	anteroventral
51 <i>b</i>	St Arnaud, Algeria 1948–1–1	right	medial	dorsal

Once correct orientation has been achieved, three major shapes are apparent in the posterior ossicones of the specimens from Olduvai and appear to be typical of ossicones from other African sites also.

Type A

The posterior ossicone extends outwards and backwards, then perhaps slightly upwards. Flanges and knobs are present on the anterior and lateral surfaces. Torsion is only slight (Fig. 3).

Olduvai examples: FLK S 1, Old.63 BK II 431, Old.5.53, M.14955, M.14954b.

Type B

The ossicone extends outwards, then upwards, then inwards and forwards. The distal tip of the ossicone is thus bent forward and sited in front of the anterior flanges on the proximal portion of the ossicone. Flanges and knobs are sited on the anterior (and, through torsion, outer) edge of the ossicone, but a knob is also present on the posteroventral edge (diametrically opposite to the proximal flange) in the proximal portion of the ossicone (Fig. 4).

Olduvai examples: BK II 068/5746 (= Old.1.53), BK II 068/5747 (= Old. 2.53), BK II 068/5753.

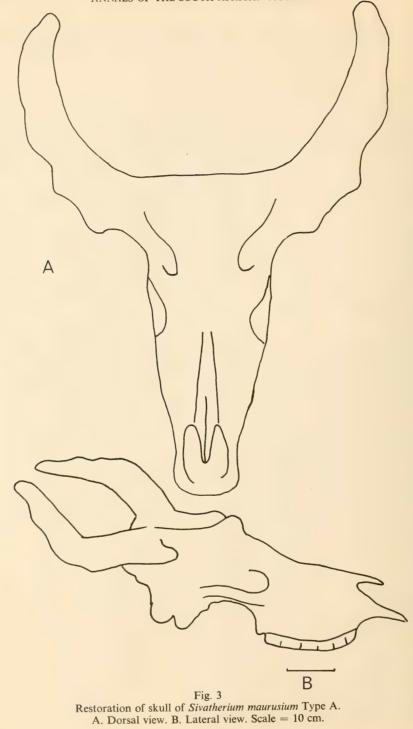
Type C

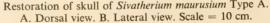
Recognizable parts of the cranium have not been observed attached to ossicones of this type. These ossicones are straight and, it is believed, point directly backwards. Knobs may be present on both medial and lateral edges but are more abundant (and more prominent) on the lateral edges (Fig. 5).

Olduvai examples: Old.68 BK II S.34, Old.53 BK II 86.

Singer & Boné (1960: 494) commented on the variability of the posterior ossicones from Olduvai and suggested that the ossicones exhibiting extreme torsion might possibly represent male specimens. Colbert (1935: 342) agreed with earlier workers that *Sivatherium giganteum* lacked ossicones in the female. It is likely that this also applied to other species of *Sivatherium* and, if this view is correct, all African sivatheriine ossicones are from male animals. Disparity in size and development of the knobs and flanges may represent individual variation, but it is also possible that the amount of secondary bone apposition, in the form of ornamentation, might be a function of the age of the individual.

All the *Sivatherium* posterior ossicones so far collected from Olduvai fall. into one of the three morphological groups listed above. It may be that these three groups possess taxonomic significance and certainly the two pairs of associated left and right ossicones (Old.1.53+Old.2.53 and FLK S 1) are symmetrical. Of the two posterior ossicones on the East Rudolf skull, however, the right ossicone falls into Group A and the left into Group B. Material collected from Olduvai subsequent to the publication of Singer & Boné's monograph includes a large number of sivatheriine postcranial elements. These are currently being investigated and it will be interesting to see whether the presence of more than one species of *Sivatherium* is indicated.





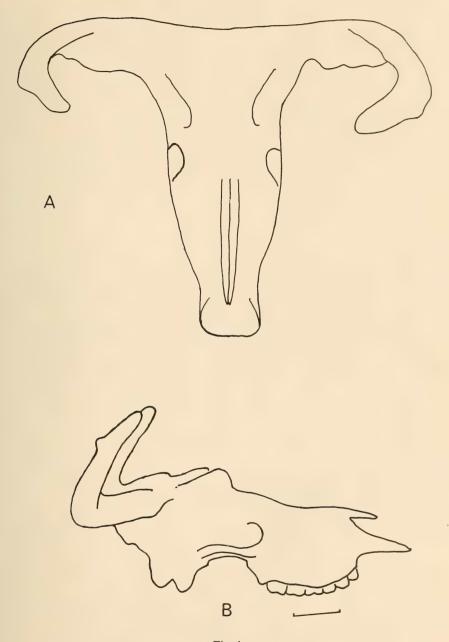
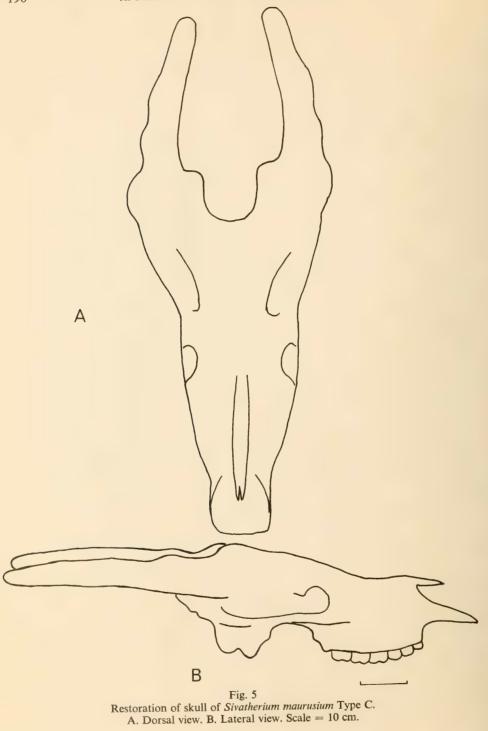


Fig. 4 Restoration of skull of *Sivatherium maurusium* Type B. A. Dorsal view. B. Lateral view. Scale = 10 cm.



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ANTERIOR OSSICONES

Singer & Boné (1960: 492) described anterior ossicones of Sivatherium maurusium from Hopefield and Tierfontein. Anterior ossicones are present on the East Rudolf skull and on two Olduvai specimens (Old.68 BK II S.34 and FLK S 1). Anterior ossicones in Sivatherium giganteum are discrete forwardprojecting conical structures sited above the orbits. Those of the East African specimens appear to be flange-like ossifications sited on the lateral edges of the cranial vaults behind the orbits. There is some doubt whether the 'anterior ossicones' of the East African sivatheriines can be interpreted as discrete structures or merely represent an anterior extension, or the beginning, of the posterior ossicones. None of the East African 'anterior ossicones' are sculpted on one side by the grooves that are present in the Tierfontein specimen (C.431B) and, as such grooves are typical of the posterior ossicones, there must be some doubt about the correct identification of the Hopefield fragment.

DISCUSSION

Quite apart from the distinct possibility of further taxonomic subdivision on the basis of ossicone morphology and postcranial elements, some doubt must also be placed on the current identification to generic level of the African Plio-Pleistocene sivatheriines. As is recorded elsewhere (Harris in press), the skull of *Sivatherium giganteum* has a much shorter facial region and a deeper and wider cranial region than the East Rudolf skull. The posterior ossicones of the African sivatheriines are orientated differently and the anterior ossicones, if interpreted as such, are sited more posteriorly and are less prominently developed. The teeth of the African and Asian sivatheriines are, however, similar in morphology.

It is possible that *Sivatherium maurusium* and *S. cingulatum* may be only specifically distinct from *S. giganteum*. It is also possible that, because the Asian sivatheriine genera overlap considerably in morphology except for their ossicones (Singer & Boné 1960: 520), the different skull shape and ossicone orientation of the African specimens may warrant generic distinction from their Asian relatives. Such major taxonomic realignment must, however, await the results of current investigations into the postcranial anatomy of the African sivatheriines, revision of the Asian forms, and, if possible, retrieval of further specimens from African sites.

SUMMARY

Isolated ossicones of *Sivatherium maurusium* can be orientated by means of their ornamentation, torsion and cross-section. Three basic shapes of posterior ossicone have been observed. The presence of a well-developed anterior ossicone in this taxon is doubtful.

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